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11 Blue Grouse

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Blue Grouse

Dendragapus obscurus (Say) 1823

OTHER VERNACULAR NAMES

*D*USKY grouse, fool hen, gray grouse, hooter, mountain grouse, pine grouse, pine hen, Richardson grouse, sooty grouse.

RANGE

From southeastern Alaska, southern Yukon, southwestern Mackenzie, and western Alberta southward along the offshore islands to Vancouver and along the coast to northern California, and in the mountains to southern California, northern and eastern Arizona, and west central New Mexico (*A.O.U. Check-list*).

SUBSPECIES (*ex A.O.U. Check-list*)

D. o. obscurus (Say): Dusky blue grouse. Resident in the mountains from central Wyoming and western South Dakota south through eastern Utah and Colorado to northern and eastern Arizona and New Mexico.

D. o. sitkensis Swarth: Sitkan blue grouse. Resident in southeastern Alaska south through the coastal islands to Calvert Island and the Queen Charlotte Islands, British Columbia.

D. o. fuliginosus (Ridgway): Sooty blue grouse. Resident from the boundary between Yukon and Alaska south through the mainland of southeastern Alaska, coastal British Columbia including Vancouver Island, western Washington, and western Oregon to northwestern California.

D. o. sierrae Chapman: Sierra blue grouse. Resident on the eastern slope of the Cascade Mountains of central Washington south into California and from southern Oregon south along the Sierra Nevada into California and Nevada.

D. o. oreinus Behle and Selander: Great Basin blue grouse. Resident in mountain ranges of Nevada and Utah.

D. o. howardi Dickey and van Rossem: Mount Pinos blue grouse. Resident on the southern Sierra Nevada from about latitude 37° N. to the Tehachapi range and west to Mount Pinos, where extremely rare.

D. o. richardsonii (Douglas): Richardson blue grouse. Resident from the southern Yukon and Alaska south through interior British Columbia to the Okanagan Valley and western Alberta to Idaho, western Montana, and northwestern Wyoming.

D. o. pallidus Swarth: Oregon blue grouse. Resident from south central British Columbia south through eastern Washington to northeastern Oregon.

N.b.: Three of the forms listed (*sitkensis*, *fuliginosus*, and *sierrae*) are sometimes specifically separated from the remaining ones and tend to have eighteen rather than twenty rectrices, yellowish rather than grayish downy young, and certain other minor structural differences.

MEASUREMENTS

Folded wing (unflattened): Adult males, 196–248 mm; adult females, 178–235 mm (adult males of all races average over 217 mm; females, under 216 mm).

Tail (to insertion): Adult males, 131–201 mm; adult females, 111–59 mm (adult males average over 150 mm; females, under 150 mm).

IDENTIFICATION

Adults, 17.2–18.8 inches long (females), 18.5–22.5 inches long (males). This is the largest of the coniferous-forest grouse of the western states and provinces. Sexes differ somewhat in coloration, but both have long, squared, and relatively unbarred tails (pale grayish tips usually occur in both sexes of all races except *richardsonii* and *pallidus*, which sometimes have suggestions of a pale tip). Upperparts of males are mostly grayish or slate-

colored, extensively vermiculated and mottled with brown and black markings, and the upper wing surfaces are more distinctly brown. White markings are present on the flanks and under tail coverts, and feathering extends to the base of the middle toe. The bare skin over the eyes of males is yellow to yellow orange, and the bare neck skin exposed during sexual display varies from a deep yellow and deeply caruncled condition (in the *fuliginosus* group) to purplish and somewhat smoother (in the *obscurus* group). Females have smaller areas of bare skin and are generally browner overall, with barring of mottling on the head, scapulars, chest, and flanks.

FIELD MARKS

Blue grouse are likely to be confused only with the similar but smaller spruce grouse, the ranges of which overlap in the Pacific northwest. Male blue grouse lack the definite black breast patch of male spruce grouse. Female blue grouse have relatively unbarred, grayish underparts, as compared with the spruce grouse's white underparts with conspicuous blackish barring. A series of five to seven low, hooting notes is frequently uttered by territorial males in spring.

AGE AND SEX CRITERIA

Females may be recognized by barring on the top of the head, nape, and interscapulars which is lacking in adult males (Ridgway and Friedmann, 1946), and by the bases of the neck feathers around the air sacs, which are grayish brown rather than white. The sex of adults may be determined from the wings alone; females have a more extensively mottled brownish pattern on their marginal upper wing coverts; in males these feathers are gray, with little or no mottling (Mussehl and Leik, 1963).

Immatures (in first-winter plumage) may be recognized by one or more of the following criteria: the outer two primaries (retained from the juvenal plumage) are relatively frayed and more pointed (van Rossem, 1925) as well as being lighter and more spotted than the inner ones, the outer tail feathers are narrow and more rounded (up to 7/8th inch wide at ½ inch below tip, as opposed to being at least 1¼ inch wide in adults), and the tail is shorter than in adults (the maximum length of plucked feathers of juvenile males is 152 mm, of juvenile females, 134 mm, compared with 162 and 138 mm in adult male and female *fuliginosus* (according to Bendell, 1955b). Immatures of both sexes generally resemble adult females but may usually be recognized by their pale buffy or white breasts, the absence of a gray area on the belly, and (except in *richardsonii* and *pallidus*) the

absence of a gray bar at the end of the tail (Taber, in Mosby, 1963).

Juveniles (in juvenal plumage) may be distinguished by the conspicuous white (tinged with tawny) shaft streaks of the upperparts, wings, and tail, and the brown rectrices which may be mottled or barred and lack a gray tip (Ridgway and Friedmann, 1946). The juvenal plumage is carried only a very short time in this species as in other grouse, and the juvenal tail feathers are molted almost as soon as they are fully grown.

Downy young are illustrated in color plate 61. Considerable variation in downy coloration exists among the numerous races (Moffitt, 1938). Downy blue grouse lack the chestnut crown patch of spruce grouse, exhibiting instead irregular black spotting over the crown and sides of the head and a conspicuous black ear patch. The black head marking in young blue grouse also includes a central crown mark that connects with frontal spotting, two indefinite lateral stripes, and a faint brownish area posteriorly that is bordered by slightly darker markings (Short, 1967). This species is thus intermediate between the extreme type of head markings found in the sage grouse and the more *Lagopus*-like markings typical of the spruce grouse.

RANGE AND HABITAT

The over-all North American range of the blue grouse is closely associated with the distribution patterns of true fir (*Abies*) and Douglas fir (*Pseudotsuga*) in the western states (Beer, 1943). Its range more closely conforms with that of the Douglas fir than any other conifer tree species, but this is probably a reflection of both species' being closely adapted to a common climatic and community type rather than any likelihood of the blue grouse's being closely dependent on Douglas fir. The species actually occupies a fairly broad vertical range in the western mountains, breeding at lower elevations, sometimes as low as the foothills, and spending the fall and winter near timberline or even above it. Rogers (1968) reports that in Colorado the birds are usually to be found at between 7,000 and 10,000 feet but have been seen at elevations as low as 6,100 feet and as high as 12,400 feet, averaging about 9,000 feet. At least in the moist Pacific northwest, lumbering and fire produces a more open forest that improves the breeding habitat of blue grouse by opening the forest cover, but heavy grazing on lower slopes can be deleterious (Hamerstrom and Hamerstrom, 1961).

In contrast to several grouse species, no major range changes of importance have occurred in the blue grouse in historical times (Aldrich, 1963). In none of the states and provinces where the species occurs is it in danger of extirpation, although the southern populations in New Mexico and Arizona are relatively sparse and scattered.

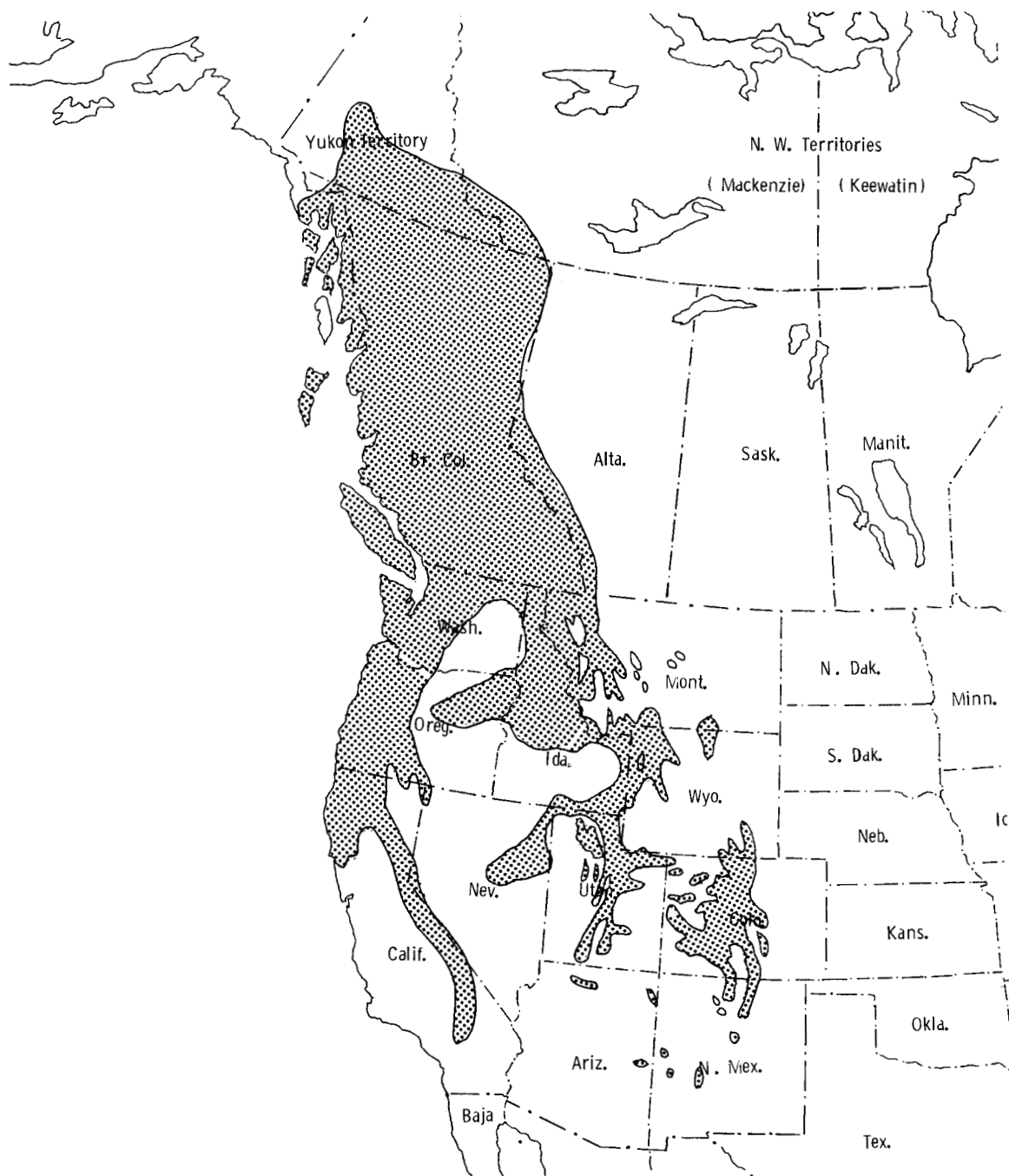


FIGURE 24. Current distribution of the blue grouse.

Although the blue grouse depends heavily on coniferous cover for wintering, its preferred habitat also includes a number of deciduous tree species, shrubs, and forbs. Foremost among broadleaf trees are aspens (*Populus*), and a variety of shrubs provide food and escape cover. Rogers (1968) summarized records of dominant trees, shrubs, forbs, and grasses associated with blue grouse observations in Colorado over a several year period. In all years, aspen was the dominant tree, snowberry (*Symphoricarpos*) was the dominant shrub, brome grass (*Bromus*) was the dominant grass, and groundsel (*Senecio*) or vetch (*Astragalus*) were the dominant forbs. Trees recorded less frequently were juniper (*Juniperus*), spruce (*Picea*), Douglas fir, and ponderosa pine (*Pinus ponderosa*). Although hens and broods were sometimes seen in piñon pine (*Pinus edulus*) and juniper cover, summer concentrations of males were usually in open coniferous stands of spruce and fir. Rarely were blue grouse seen more than a mile from trees or shrubs, and females with broods were usually not far from water.

Similar observations on blue grouse habitat characteristics have been made in southern Idaho by Marshall (1946). There the vertical range used by the species extends from less than five thousand feet in ponderosa pine-Douglas fir forest, which is infrequently used by blue grouse, to subalpine forests reaching over eight thousand feet, which provide wintering areas for both sexes and summering habitats for males. In these higher ridges they use the conifers, especially Douglas fir, for both food and cover. In all but eight of twenty-five cases, the grouse were observed to land in conifers on being flushed, while the remainder landed on the ground. Of 159 observations of birds as to cover type, 87 were in Douglas fir, 41 were in subalpine cover, 25 were on banks of streams, and the remaining 6 were in grass or brush cover.

A study by Fowle (1960) on Vancouver Island provides comparable data for the coastal population of blue grouse. Summer habitat there consists of second-growth cover produced by fire and logging of Douglas fir forests. About 45 percent of the sample areas had no vegetation at all, while in the rest mosses, lichens, ferns, and grasses, as well as a variety of shrubs and forbs, made up most of the cover. Except near water, where alders (*Alnus*), willows (*Salix*), and dogwood (*Cornus*) occurred, trees were only in scattered groups. About 20 percent of the area was covered with important grouse foods, including bracken fern (*Pteridium*), willow, Oregon grape (*Mahonia*), blackberry (*Rubus*), huckleberry (*Vaccinium*), salal (*Gaultheria*), and cat's-ear (*Hypochaeris*). These plants made up a total of more than 90 percent of adult food samples, and over 80 percent of juvenile food samples.

By the end of September, the birds move up to higher slopes, and they winter in the coniferous zone (Bendell, 1955c), where they are found primarily in subalpine forests. Zwickel, Buss, and Brigham (1968) point out that winter habitat is probably determined more by cover type than by altitude per se and may occur in Washington at as low as four thousand feet, between the ponderosa pine and Douglas fir zones, with the critical factor apparently being the presence of interspersed Douglas and true firs.

POPULATION DENSITIES

Estimates of blue grouse population densities are difficult because of the cover inhabited by the species, and the generally solitary nature of the species. Rogers (1968) summarized results of grouse surveys from vehicles; over a three-year period in two study areas they averaged one grouse per 26.07 miles, ranging from 10.3 to 38.72 miles in various years.

Using a strip-count census method, Fowle (1960) counted adult grouse on Vancouver Island during two summers. In four areas totaling 272 acres he determined a density in 1943 of 2.6 acres per bird. Later work in the same area by Bendell and Elliott (1967) indicated that the density of territorial males in dense and sparse populations respectively was approximately 0.44 and 0.13 or less males per acre, or from about 2.3 to 7.7 acres per territorial male. Similar counts of territorial male blue grouse were made by Mussehl and Schladweiler (1969) in Montana on six study areas that were in part exposed to insecticide spraying. Numbers of territorial males on sprayed and unsprayed areas did not appear to differ and averaged about 1 male per 18 acres, ranging from 12 to 24 acres per male.

Whether the blue grouse is subject to population "cycles" is perhaps questionable, but at least major population fluctuations and corresponding changes in density evidently do occur. Fowle (1960) and Hoffmann (1956) summarized historical data on grouse populations during the 1900s but neither attempted to explain these fluctuations. Zwickel and Bendell (1967) hypothesized that population fluctuations in the species are related to the nutritional condition of females, as determined by the summer range conditions, which might affect chick survival and in turn determine subsequent autumn population densities. However, no relationship was found between the number of young in autumn and the breeding density in the following year. They suggest that the death rate or dispersal of juveniles between autumn and early spring is the single most important factor regulating breeding densities.

HABITAT REQUIREMENTS

Wintering Requirements

Primary wintering needs for the blue grouse appear to be sufficient trees to provide roosting and escape cover and a supply of needles from trees of the genera *Abies*, *Tsuga*, or *Pseudotsuga* as a source of food. Beer (1943) reports that adult blue grouse subsist almost entirely on needles from November through March. Needles, buds, twigs, and seeds of Douglas fir may all be eaten in winter, and needles, buds, and pollen cones of true fir are also used. Where both *Abies* and *Pseudotsuga* are present, the former appears to be preferred. Larches (*Larix*) may be used until its needles are shed, and various species of pines are used for their buds, pollen cones, and seeds. Marshall (1946) noted that 99 percent of the contents of nine birds killed during winter in Idaho consisted of needles and buds of Douglas fir. Interestingly, grit is evidently retained in the gizzard through the winter, in spite of the deep snow cover. Hoffmann (1956) reported that white fir (*Abies concolor*) provided favored winter roosts in California.

Spring Habitat Requirements

As the winter ends, both sexes begin to move downward from the coniferous zones, and males seek out areas suitable for territories. Bendell and Elliott (1966) analyzed the habitats used by both sexes of blue grouse on Vancouver Island from spring through August, classifying cover as "very open" (40 percent tree, log, stump, and salal cover) or "very dense" (100 percent woody cover). The relative grouse use in two types was 115 in very open cover compared to 18 in very dense cover. The use of the very dense cover was limited to some territorial males that apparently established territories there before it became so heavily vegetated and some females. The authors concluded that the blue grouse is better adapted to a dry habitat than is the ruffed grouse and may indeed have evolved from a grassland species. Supporting this view was their finding that young captive blue grouse required only about half as much water as captive ruffed grouse. They concluded that the breeding habitat of blue grouse might be defined as open and dry, with shrubs and herbs interspersed with bare ground.

In California, Hoffmann (1956) found that the persistence of snow cover determined the onset of hooting in spring and the transition to spring behavior in a study area where virtually no seasonal migration occurred. Blackford's studies (1958, 1963) on Montana provide additional information on territorial requirements for an interior population (*obscurus*) of this species. In this area, hooting occurred either at ground level or in trees

during strutting. Strutting areas were in forest-edge habitats with combined grassy, open forest border and a dense coniferous stand. Occasionally, rocky outcrops occurred, and old logs were present on the forest floor. Blackford's observations established that earlier, widely reported differences in territorial defense and strutting behavior between coastal and inland populations of blue grouse are not in general absolute.

Yearling males may migrate downward to the breeding areas or may remain on the wintering areas through the summer. Bendell and Elliott (1967) estimated that about half of the yearling males moved to the summer range their first year. There they are silent, move about widely, and may be attracted to hooting territorial males. These authors observed two cases of territorial yearling males. Females may return to the same general area of the summer range in subsequent years, but are not nearly so localized in this respect as are males (Bendell, 1955c). Unlike males, females are not particularly aggressive to one another, and their home ranges may overlap. However, Stirling (1968) suggested that during the squatting and egg-laying periods females do become somewhat aggressive, and this behavior tends to scatter females and perhaps allows for a spacing of nests.

Nesting and Brooding Requirements

Surprisingly little has been written on specific nesting needs for blue grouse, perhaps because their nests are rather difficult to locate. Usually the nest is located near logs or under low tree branches and is fairly well concealed. Bendire (1892) stated that most nests are under old logs or among roots of fallen trees and are generally to be found in more open timber along the outskirts of the forest. He found one nest beside a creek in rye grass some two miles away from timber and another in an alpine meadow under a small fir tree, with no other trees within thirty yards. Bowles (in Bent, 1932) noted that nests are usually in very dry, well wooded sites, and they are often at the bases of trees or under fallen branches or some other shelter. However, they may be up to one hundred yards from trees, with little or no concealment. Lance (1970) found that nests were usually fairly near territorial males but well separated from the nests of other females.

Brooding habitat for blue grouse appears to be that which provides ample opportunities for the young to feed on insects and other invertebrates. Beer (1943) suggested that blue grouse usually nest in open situations where there will be an abundance of insect life for the newly hatched birds. For the first ten days, the young feed almost exclusively on animal material, especially ants, beetles, and orthopterans, according to Beer. As the young grow older, berries, such as currants (*Ribes*) and Juneberries (*Amelanchier*)

are sought out, and the young birds and adults gradually move upwards as they follow the ripening berry crop.

Wing, Beer, and Tidyman (1944) reported that broods occupy home ranges that are characterized by semiopen vegetation and available water. Relatively open areas are used by newly hatched chicks, while older broods move into more densely vegetated areas. Mussehl (1963) found that brood cover in Montana is consistently low (averaging seven to eight inches), has little bare ground (8 to 20 percent), and is predominantly herbaceous in nature, with grasses next in importance, followed by low shrubs and forbs. Woody cover increases in importance for food and escape cover as the birds mature.

FOOD AND FORAGING BEHAVIOR

In spite of the rather broad geographic range of the blue grouse, its food requirements appear to be fairly consistent. Martin, Zim, and Nelson (1951) report that Douglas fir was the most important food item in 158 samples from the northern Rocky Mountains, and in 154 samples from the Pacific northwest Douglas fir and true firs provided the major food items. They also list a variety of herbaceous plants and sources of berries that are used in summer and fall. Judd (1905b) indicated that winter blue grouse foods include ponderosa pine, Douglas fir, true firs (*Abies concolor* and *A. magnifica*), and hemlocks (*Tsuga heterophylla* and *T. mertensiana*).

Beer (1943) analyzed over one hundred crops and gizzards of blue grouse mostly from Washington and Oregon, and noted that adult foods were 98 percent plant materials, with conifer needles comprising 63.8 percent, berries 17 percent, miscellaneous plant materials 17.2 percent, and animal material 1.7 percent of the specimens examined. Beer noted that the grouse reach the peak of their morning feeding by 7 A.M. and stop by 9 A.M. Later feeding periods are just before noon, during late afternoon, and particularly toward evening, when the most intensive foraging of the day occurs. Growing young feed more continuously than adults, but those of all ages forage most heavily during the last three hours of daylight. Similar observations were made by Fowle (1960), who noted that although feeding occurred through the day, the greatest amount of food was consumed in the evening after 6 P.M. Males often alternate feeding with hooting, but females with young evidently restrict their foraging to the evening. Fowle never saw wild grouse drink water and believed it might not be important when berries or other succulent foods are available.

Hoffmann (1961) noted that blue grouse in California rely during the winter almost entirely on needles of white fir (*Abies concolor*), which he

analyzed for protein content. He found that needles from high in the tree had a higher protein content than those from lower branches but that no apparent yearly differences occurred over a three-year period during which the grouse population suffered a major decline.

MOBILITY AND MOVEMENTS

Seasonal Movements.

The altitudinal movements of blue grouse to coniferous wintering areas has been reported for most areas; the exception being Hoffmann's study in California (1956). Doubtless the horizontal distances involved in movements between summering and wintering areas differ greatly in various regions, but relatively little detailed information is available. One banding study by Zwickel, Buss, and Brigham (1968) in north central Washington indicates that autumn migrations of blue grouse may be fairly long. The longest movement recorded by a banded bird was 31 miles, which occurred in less than two months. Of 30 birds recovered, 50 percent had moved over 5 miles, and 30 percent were recovered over 10 miles from where they had been banded. In contrast, Mussehl (1960) reported a maximum fall movement of 3.4 miles in Montana, while Bendell and Elliott (1967) found a maximum fall movement of 10 miles on Vancouver Island. Zwickel, Buss, and Brigham speculated that at least some breeding females leave their broods behind and return to their previous wintering areas, which stimulates wandering by young birds and the possible colonization of new wintering areas.

Daily Movements.

Evidently relatively little daily movement is performed by adult male blue grouse from the time they arrive on the summer range and establish territories until they begin their fall movement back to the wintering areas. Males probably establish territories as soon as weather conditions permit, and maintenance activities such as foraging, dusting, and sleeping are all carried out within the territorial boundaries (Bendell and Elliott, 1967). Territorial size presumably varies inversely with population density. In dense populations of about 0.44 males to the acre, Bendell and Elliott estimated that territorial sizes averaged about 1.5 acre. In sparse populations of about 0.13 males to the acre, territories were at least 5 acres in size.

Similarly, female grouse probably exhibit little daily movement, at least after fertilization has occurred. Until then they presumably move about through the territories of males until sufficiently stimulated to permit mating. Various studies of marked broods (Mussehl, 1960; Mussehl and Schladweiler, 1969) indicate that prior to dispersal the broods move about relatively little, and individual brood ranges may overlap considerably.

REPRODUCTIVE BEHAVIOR

Territorial Establishment

Male blue grouse evidently become territorial immediately after their arrival on the breeding range (Blackford, 1963) or as soon as snow cover conditions permit (Hoffmann, 1956). Territorial site requirements are somewhat ill-defined and may vary locally or with subspecies. In Colorado, Rogers (1968) states that display sites may be in aspen-ponderosa pine, mixed fir and aspen, open and dense aspen, mixed shrubs, sagebrush, wheat fields, and on roadbeds, but preference is shown for fairly open stands of trees or shrubs. Physical features include earth mounds, rocks, logs, cut banks, and occasionally tree limbs. Preference is generally given to flat, open ground, although steep slopes are also used. Display sites may be near heavy cover, but this is normally used for escape rather than for display. Two observations were made of birds displaying at more than twenty feet, but ground display is typical of interior populations of blue grouse.

In contrast, Hoffmann (1956) found that in a California population (*fuliginosus*) the males normally hooted from the tops of white fir or sometimes from Jeffrey pine (*Pinus jeffreyi*) or lodgepole pine (*P. contorta*). Bendell and Elliott (1966, 1967), studying the same subspecies on Vancouver Island, found that many hooting sites were elevated areas on the ground and that territories included diverse cover types, with males hooting from virtually all types of cover within their territory. In dense cover with small openings, territories are related to the location of openings. Thickets within territories are used for resting and concealment. This combination of open areas for display and shelter in the form of fir clumps, logs, or stumps used for hiding and as observation posts provides the basic territorial requirements. Several display sites may be used within a single territory; Rogers (1968) noted that from two to eleven hooting sites for one bird have been recorded.

Territorial Advertisement

Territorial proclamation by male blue grouse is achieved by a combination of postures, vocalizations, and movements that are collectively called hooting. In spite of reported differences in hooting behavior among different populations, current evidence indicates that actual differences are few and tend to be quantitative rather than qualitative. Thus, the interior populations (dusky grouse) have much weaker hooting calls that are barely audible more than fifty yards away, whereas the coastal populations (sooty grouse) have strong hooting notes that carry several hundred yards. The former typically call from the ground but may use trees, while the latter more often call from tree limbs. The gular sac of dusky grouse males is generally purplish, while that of sooty grouse is more heavily wrinkled and yellowish. The eye-combs of dusky grouse are large and vary from yellow to a bright red under maximum stimulation; those of sooty grouse are smaller and usually are lemon yellow, but sometimes also become livid red (Bendell and Elliott, 1967).

During hooting the male partially raises and spreads his tail and opens the feathers of his neck to expose an oval gular sac that is surrounded by white-based neck feathers, forming a "rosette" pattern. Both wings are slightly drooped toward the ground. In this posture (called the "oblique" by Hjorth, 1970) the gular sac is partially inflated in a pulsing manner as up to seven but usually five (in the dusky grouse) or six (in the sooty grouse) *hoot* sounds are uttered in fairly rapid succession. These are repeated at frequent intervals. Bent (1932) reported intervals of 12 to 36 seconds between call sequences of *fuliginosus*, Steward (1967) determined a mean interval of 24.2 seconds in *sitkensis*, and Rogers (1968) noted intervals of from 6 to 23 seconds for *obscurus*. Such hooting is uttered at various times during the day, but is most prevalent in early morning and again in late evening, primarily between 3 and 5 A.M. and again between 7 and 10 P.M. (Bendell, 1955c). Hjorth (1970) noted that although in both subspecies groups the call sequence lasts about three seconds, the fundamental frequencies of dusky grouse calls (95 to 100 Hz.) are lower than those of sooty grouse (100 to 150 Hz.) and have much less amplitude. Males may periodically move about between hooting sites, and while walking they keep the head low and the tail cocked and spread, exposing the spotted under tail coverts ("display walking" of Hjorth, 1970).

Strutting Displays

When in the presence of another grouse, the male stands in an erect posture with his tail tilted toward the other bird ("upright cum tail-tilting"

of Hjorth, 1970), the eye-combs enlarged, and the wing away from the intruder drooped in proportion to the amount of tail-tilting. In this posture the male may perform vertical head-jerking movements, with the gular sac nearer the intruder expanding in synchrony with these head movements (Hjorth, 1970). Hjorth also reported that these downward head movements ("bowing cum asymmetric apteria display") may be greater in the dusky grouse group than in sooty grouse.

In this erect and tilted-tail posture, the male typically advances toward the intruder. Bendell and Elliott (1967) stated that in the sooty grouse the head and neck are held broadside to the other bird in such a way as to be framed against the background of the dark tail. Rogers (1968) has a photograph of the comparable posture of a Colorado dusky grouse. The approach display is climaxed by a quick, arcing dash toward the other bird ("rush cum single hoot" of Hjorth, 1970), which is associated with maximal tail-cocking and spreading, extreme engorgement of the eye-combs, and a drooping of the wings so that they drag on the ground. In this posture the male jerks his head several times, then lowers it and runs forward with short, fast steps, terminating the run with a deep *oop* or *whoot* note. Rogers (1968) noted that this sound could be heard as far as 510 feet away, in contrast to the hooting series in Colorado grouse, which could not be heard beyond 105 feet. Bendell and Elliott (1967), as well as Hjorth (1970), observed that it is actually a double note, with a short squeal or whistle following the deeper sound. Hjorth (1967, 1970) noted that during the forward dash the male deflates his neck, turns his tail toward the other bird, and holds his neck in such a way that the cervical rosette is maximally exposed. The head is held low, the tail is twisted to provide maximum surface exposure, and the wing on the far side is increasingly drooped as the tail is twisted. After the call is uttered the bird gradually assumes a normal posture again.

If the other bird is a receptive female she may remain in place, and the male then displays about her, raising and lowering his body and jerking his head, always keeping the neck rosette and nearer eye-comb in full view of the female. After two or three minutes of such display, the male moves behind the female and attempts to mount her. During treading the male grasps the nape of the hen in his beak, and holds her body against his lowered wings as she squats. Following treading the male again assumes his upright display posture (Hjorth, 1970).

Flight Displays

The other primary aspects of display by male blue grouse involve fluttering or flying movements which have been variably ritualized to produce

sound and advertise the presence of the male. They are difficult to classify, since they have been described differently by various observers. Blackford (1958, 1963) attempted to classify these aerial displays based on his observations in Montana, which may be summarized as follows:

"Wing-fluttering" is a brief flapping of wings as the bird rises about eight or ten inches in the air, producing relatively little noise. It may be performed by either sex, both on the ground and in trees.

"Wing-drumming" is the typical male display flight, or flutter jump. It is a short, vertical leap into the air as the bird beats his wings strongly a few times before descending. Often one wing is beat much more strongly than the other, producing a rotary movement ("rotational drumming") and causing the bird to make an incomplete turn before landing.

"Wing-clapping," so far noted only by Blackford, is an upward leap associated with a single, very loud wing note.

"Drumming flight" was distinguished by Blackford from normal wing-drumming by the fact that a circular flight some ten to twelve feet in diameter is made before landing again near the takeoff point.

Several other possible wing signals were noted by Blackford (1963), including a "double wing flutter," a "perching signal," an "explosive flush," and an "aerial signal." Since they have not been well studied or described by others, they need not be given further consideration here.

Vocal Signals

Male vocalizations other than the *hoot* and *oop* calls are relatively few, judging from most accounts. Rogers (1968) reported a "gobbling" sound uttered by a male after making a clapping wing-beating flight to a branch. This was followed by regular hooting sounds until a single two-note *ca-caw* was uttered about eighteen minutes later.

Female vocalizations reported by Blackford (1958) include an in-flight alarm call, *kut-kut-kut*, a low warning note uttered before flight, *kr-r-r*, and an "excitement" call, *kutter-r-r-r*, which fluctuates greatly in pitch. Rogers (1968) noted that the in-flight alarm call of females was the note most commonly heard. Female blue grouse also produce a "whinny" call that is highly effective in stimulating males to begin hooting and to move toward the source of the sound. Use of tape-recordings of such calls is an effective method of censusing blue grouse (Stirling and Bendell, 1966). Likewise, recorded chick distress calls evoke clucking responses from broody hens.

Stirling and Bendell (1970) have recently reviewed the behavior and vocalizations of adult blue grouse. They described and presented sonagrams of three male calls, including the hooting call, the *whoot* call associated

with the rush display, and a growling *gugugugug* associated with attack. Females were believed to have two calls related to reproduction: the "whinny," related to copulation readiness and the "quaver call" or *qua-qua* that consists of a pulsed series of notes produced by breeding females just prior to the time that males reach maximal reproductive development, thus possibly synchronizing breeding cycles. Females also utter a "hard cluck" or *bruck-duck* call, which apparently serves as a threat signal.

Collective Display

Although blue grouse are regarded as a species which normally defends fairly large territories and displays in a solitary fashion, several observations of collective display have been made. Bendell and Elliott (1967) noted that of 420 territorial males studied, the average distance between nearest territorial neighbors in open cover was approximately six hundred feet. In 5 percent of the one thousand-foot circular areas they studied there were seven or eight hooting males, which were usually two hundred to five hundred feet apart and formed a "hooting group" that usually called in chorus. They regard such hooting groups as indicating a habitat favorable for territories rather than as a variant of lek behavior, since, they point out, blue grouse remain on their territories through the breeding season, in contrast to typical lekking grouse. However, Blackford's observations (1958, 1963) of collective display indicated that males will leave their territorial sites and cross over adjacent territories to perform in a "communal court." In one case he noted that at least two males, two females, and one bird of unknown sex converged on the territory of another male, where collective display occurred. This kind of temporary establishment of collective display areas by males which perhaps follow females into the territory of an unusually effective resident male might provide the evolutionary basis for typical lek behavior, provided that such "hooting groups" are more efficient in attracting females than are individual males displaying in a solitary fashion.

Nesting and Brooding Behavior

Since the male plays no role in nest defense, incubation, or brooding, the female undertakes these duties alone. Evidently nearly all females, including yearlings, attempt to nest (Zwickel and Bendell, 1967). Further, most hens that fail to produce a brood of young do so because of nest destruction rather than nest desertion. Zwickel and Bendell (1967) found that of thirty nests found, twelve hatched successfully, eight had been

deserted, and ten had been destroyed. The deserted nests were attributed to human disturbance. In that area, foxes and weasels were suggested as principal nest predators. How much renesting might occur after nest destruction or desertion in blue grouse is still uncertain, but Zwickel and Lance (1965) reported two definite instances indicating that renesting might occur even when the first nest is destroyed late in incubation and that a second clutch can be started within about fourteen days after such destruction.

Zwickel and Bendell (1967) found that fifty-one nests contained 323 eggs, or an average clutch size of 6.3 eggs. Gabrielson and Jewett (1940) reported that nine nests contained 74 eggs, averaging 8.2 eggs per clutch. Zwickel and Lance (1965) indicate that the laying rate for blue grouse is 1.5 days per egg and that the incubation period is 26 days.

Upon hatching, blue grouse chicks become fairly independent of the female relatively soon. Zwickel (1967) found that chicks began to eat plant materials at one day of age, can fly at six to seven days of age, and by two weeks of age can fly up to sixty meters. No chicks older than eleven days were observed being brooded by the hen, and few over seven days old were seen being brooded. Contrary to other writers, Zwickel (1967) doubts that chilling by rain or cold days normally plays an important role in chick survival. Zwickel noted several calls of brooding females. When the chicks wailed loudly with their distress note, the females uttered a low brood call, *cu-cu-cu*. While foraging, hens produced a similar but less audible series of notes that Zwickel terms a contact call. When calling the brood together, the female sometimes produced a high-pitched *kwa-kwa-kwa* call which the chicks responded to by wailing. When the hen returned to her brood after a considerable absence she would cluck loudly or produce a high-pitched *kweer-kweer-kweer* which was audible for up to $\frac{1}{4}$ mile under favorable conditions. Zwickel concluded that vocal signals were highly important in maintaining brood organization and exhibited considerable plasticity to meet varying needs.

Evidently most chick losses occur during the first two weeks of age, according to Zwickel and Bendell (1967). These authors present data indicating that brood sizes for chicks up to fourteen days old average from 3.3 to 4.4 young, while brood sizes for chicks estimated to be older than forty-two days average 2.9 to 3.7 young. Mussehl's study in Montana (1960) indicated that the movements of eight marked broods for periods of nineteen to forty-seven days were restricted to areas having maximum diameters of 440 to 1,320 yards. During early July these broods primarily used a mixed grass-forb cover, but with gradual drying of the prairie forbs they moved into deciduous thickets for the remainder of their brooding period. Little use of montane coniferous forest was noted. By the end of

August most of the brooding range had been abandoned, and broods began to disperse. Juveniles then moved singly or in small groups, with individual birds making lateral movements of up to 2.1 miles, as they worked their way up toward the wintering ranges.

EVOLUTIONARY RELATIONSHIPS

The blue grouse presumably had its evolutionary origin in western North America, either in a coniferous forest situation or in a forest-grassland edge habitat. Jehl (1969) concluded that two species of *Dendragapus* occurred in the western United States in the late Pleistocene, one of which presumably directly gave rise to the modern blue grouse. I believe that the ancestral blue grouse probably originated in North America, whereas the ancestral spruce grouse may have had its origins in eastern Asia, only later coming into contact with the blue grouse.

It seems probable that the sage grouse also had its origin in the western part of North America and may be much more closely related to the blue grouse than the adult plumage patterns would suggest. The surprising similarities of the downy young would support this view, and the strutting behavior patterns of the two species are not greatly different. To a much greater extent than is usually appreciated, the breeding habitat of the blue grouse is relatively arid and open, and the bird is in no sense a climax coniferous forest species.

I would suggest that North America was invaded relatively early from Asia by a *Tetrao*-like ancestral type, which as it moved southward produced the more montane-dwelling blue grouse ancestor, and also the intermontane or valley-dwelling sage grouse ancestor. A second invasion brought the spruce grouse into North America, possibly as recently as late Pleistocene times.